African Invertebrates Vol. 48 (2) Pages 1–19 Pietermaritzburg December, 2007

Revision of the genus *Prestonella* (Mollusca: Gastropoda: Orthalicoidea: Bulimulidae *s.l.*), a distinctive component of the African land snail fauna

D. G. Herbert

Natal Museum, P. Bag 9070, Pietermaritzburg, 3200 South Africa, and School of Biological & Conservation Sciences, University of KwaZulu-Natal, P. Bag X01, Scottsville, 3209 South Africa; dherbert@nmsa.org.za

ABSTRACT

The familial relationships of the enigmatic southern African land snail genus *Prestonella* have recently been resolved and the genus shown to be the sole known African representative of the Gondwanan family Bulimulidae *s.l.* In this paper I present a taxonomic revision of the genus and provide further data on the distribution, habitat preferences and conservation of the species. The genus is represented by three described species, *P. bowkeri* (type species), *P. nuptialis* and *P. quadingensis*, but the validity of the latter as taxon distinct from *P. nuptialis* is doubtful. A lectotype is designated for *Bulimus bowkeri* Sowerby. The species exhibit highly fragmented, relictual distributions associated with specialised habitats along the southern edge of the Great Escarpment, and are likely to become increasingly threatened as a result of climate change.

KEY WORDS: Bulimulidae *s.l.*, *Prestonella*, southern Africa, Gondwana, taxonomic revision, conservation.

INTRODUCTION

The land snail genus *Prestonella* Connolly, 1929 is an endemic and characteristic element of the southern African terrestrial malacofauna. Three species-level taxa referable to the genus have been described, *Prestonella bowkeri* (Sowerby, 1890), the type species, *P. nuptialis* (Melvill & Ponsonby, 1894) and *P. quadingensis* Connolly, 1929. On account of its uncertain phylogenetic relationships, the genus has stood out for many decades as something of an enigma. It has been referred to a number of different families, but with minimal documented evidence and often with considerable doubt (see taxonomic history below). This uncertainty stemmed simply from the fact no information on the internal morphology of the animal was available (Solem 1959: 123) and thus data on many phylogenetically informative characters were lacking.

Since Connolly was able to figure the radula of the type species and Watson was reportedly studying its anatomy (Connolly 1929, 1939), live-collected material of *Prestonella* must have been available in the early 1900s. Watson, however, never published his morphological observations and in the intervening period no further living specimens have been collected, despite concerted effort (Bruggen 1985). Indeed very little material, even empty shells, of any of the three described species has been collected since they were originally described, none at all within the last fifty years.

To gain additional insight into the phylogenetic affinity of *Prestonella* it was thus necessary to obtain further living specimens. With this as a goal, in January 2002 and in collaboration with Mary Bursey of the East London Museum, I undertook a field trip to the Somerset East and Cradock area, Eastern Cape, South Africa, in order to search for material of *P. bowkeri* and *P. nuptialis* at sites where they were historically known to occur. Living colonies of both species were found, and specimens have subsequently been studied from both morphological and molecular perspectives.

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The phylogenetic implications of these investigations are presented in a separate paper (Herbert & Mitchell in press), and conclusively demonstrate that *Prestonella* should be referred to the Orthalicoidea: Bulimulidae *s.l.* Molecular evidence from a small pool of orthalicoid species belonging to the Amphibulimidae, Bulimulinae and Placostylinae, places *Prestonella* in a well supported, monophyletic, orthalicoid clade structured in the following manner: Amphibulimidae + (Bulimulinae + (*Prestonella* + (*Bothriembryon* + *Placostylus*))). Morphological evidence from a range of independent character suites including the protoconch, radula, jaw, distal reproductive tract and pulmonary anatomy is fully concordant with this. *Prestonella* retains many plesiomorphic morphological character states suggesting that it represents a little modified stage in bulimulid evolution, these feature it shares with bulimuline taxa from South America and with the southern Australian *Bothriembryon* Pilsbry, 1894. In contrast, the largely Melanesian *Placostylus* Beck, 1837, exhibits a number of apomorphic characters. Based on the limited number of orthalicoid taxa for which molecular data are available, it is evident that *Prestonella* shares a closer relationship to Australasian taxa than to those from South America.

The majority of recent works discussing the Bulimulidae *s.l.* have considered it to be restricted to the Americas (primarily the Neotropics) and Australasia–Melanesia, and to have no African representatives (Solem 1959, 1998; Peake 1978; Breure 1979; Schileyko 1999), in line with Pilsbry's earlier observation 'there is yet no trace of Bulimulidae in Africa' (Pilsbry 1902: ix). Despite its apparent absence in Africa (and also Madagascar and India–Sri Lanka), the family is considered to be of Gondwanan origin (Solem 1998). The morphological and molecular evidence demonstrating the bulimulid affinities of *Prestonella* thus represents the first confirmed record of the occurrence of the Bulimulidae *s.l.* (and the Orthalicoidea as a whole) in Africa (Herbert & Mitchell in press) and shows the family to have a classic tri-continental, southern hemisphere distribution.

In this paper I present a taxonomic revision of the described species of *Prestonella*, providing additional information on species characters, geographical range and habitat preferences, together with some observations on the conservation of the species and comparative data concerning the internal morphology of *P. nuptialis*.

TAXONOMIC HISTORY

When describing what was to become the type species of *Prestonella*, Sowerby (1890) did not specify its familial relations, but tentatively referred it to *Mesembrinus* Albers, 1850 [= *Drymaeus* Albers, 1850], indicating that he considered it to be of bulimulid affinity. Later, Kobelt (1899–1902) chose to refer the species to the Buliminidae [= Enidae + Cerastidae], and Connolly (1912) referred it to the Enidae, but neither provided any justification. However, when subsequently proposing *Prestonella*, Connolly (1929) referred his new genus back to the Bulimulidae, basing his decision on Hugh Watson's unpublished anatomical observations. At the same time, he noted that the family was already known to occur in Africa in the form of the genus *Aillya* Odhner, 1927, which Odhner (1927) believed to be a bulimulid on anatomical grounds.

Thiele (1931) maintained the bulimulid affinities of both *Prestonella* and *Aillya*, referring them to the subfamily Amphibuliminae. Zilch (1959–60) was of a similar opinion, although he raised the Amphibuliminae to the rank of family, within the superfamily

‘Bulimulacea’ [= Orthalicoidea]. Van Mol (1978), however, subsequently investigated the internal morphology of the type species of *Aillya* (*A. camerunensis* Odhner, 1927) in greater detail, and found it to differ significantly from that of bulimulids. He considered it to represent a distinct family, perhaps derived from a stock ancestral to the Helicarionidae and Urocyclidae, rather than the elasmognaths (Succineidae and Athoracophoridae) as suggested previously by Baker (1955). Since Hugh Watson did not publish the anatomical observations on *Prestonella* to which Connolly (1929) referred, the internal anatomy of the genus has remained undocumented. Connolly’s brief notes on the jaw and illustration of the radula teeth (Connolly 1939), neither particularly informative phylogenetic characters, represented the only morphological data available. Subsequent statements regarding the familial affinities of *Prestonella* have therefore lacked firm evidence and have been based largely on unspecified features of the shell. The uncertainty surrounding the relations of the genus has been highlighted by Bruggen: in 1969 he maintained its position in the Amphibulimidae (Bruggen 1969*a*, *b*), but subsequently (Van Mol having shown that *Aillya* was not of bulimulid/amphibulimid stock) he suggested that it may in fact represent a distinct family, the Prestonellidae, perhaps

TABLE 1

Summary of history of taxonomic referral of *Prestonella* and its type species.

Author	**Suprageneric referral of *Prestonella***
Sowerby 1890	Not stated, inferred as Bulimulidae [based on position of *Mesembrinus*]
Kobelt 1899–1902	Buliminidae [= Enidae + Cerastidae]
Connolly 1912	Enidae
Connolly 1929	Bulimulidae [proposed *Prestonella* as a new genus with *Buliminus* (*Mesembrinus*?) *bowkeri* Sowerby, 1890, as type species]
Connolly 1939	Bulimulidae
Thiele 1931	Bulimulacea: Bulimulidae: Amphibuliminae
Solem 1959	*Prestonella* a dubious bulimulid
Zilch 1959–60	Bulimulacea: Amphibulimidae
Bruggen 1969*a*, *b*	Amphibulimidae
Parodiz 1969	Amphibulimidae/inae
Bruggen 1977	Related to succineids or urocyclids, or perhaps a family of its own, the Prestonellidae
Bruggen 1978	Uncertain – Succineidae, Urocyclidae or ?Prestonellidae
Breure 1979	No Bulimulidae in Africa
Bruggen 1985	?Prestonellidae
Bruggen 1986	Prestonellidae
Vaught 1989	Orthalicoidea: Amphibulimidae
Schileyko 1999	Aillyinei: Aillyidae
Herbert & Mitchell in press	Orthalicoidea: Bulimulidae *s.l.*

derived from 'the cosmopolitan succineids or the urocyclids (cf. Aillyidae)' (Bruggen 1977).

Prestonella and *Aillya* appear to be the only land snails from sub-Saharan Africa that have ever been referred to the Bulimulidae *s.l.* Following the precedent set by Odhner (1927) with regard to *Aillya*, Connolly (1929) seemed confident when referring a second African taxon, *Prestonella*, to the Bulimulidae. However, subsequent authors have not been privy to Watson's unpublished anatomical observations on *Prestonella* and, in the light of the helicarionid/urocyclid affinities of the Aillyidae (Van Mol 1978), most have dismissed the occurrence of the Bulimulidae in Africa. Presumably such reasoning led Bruggen (1985) to state that *Prestonella* was not a bulimulid/amphibulimid. Instead, Connolly's discussion of *Prestonella* together with *Aillya* has resulted in *Prestonella* being considered to some degree related to *Aillya*, and thus perhaps also referable to the Aillyidae (Schileyko 1999). Vaught (1989) was the only recent author to maintain *Prestonella* with bulimulid taxa *sensu lato*. This history is summarised in Table 1.

MATERIAL AND METHODS

The sites selected for field collecting focused on the localities listed for *Prestonella bowkeri* and *P. nuptialis* by Connolly (1939). Additional notes on old museum labels in the Natal Museum also provided valuable clues as to the more precise habitat. Details of the sites are provided in the locality data given in the following species treatments. Living specimens were drowned overnight in sealed tubes and preserved in 75% ethanol for anatomical dissection. All dissections were performed under a Wild M4 dissecting microscope with drawing tube. Radulae were extracted by maceration of the buccal mass in dilute NaOH, rinsed in distilled water, dehydrated in ethanol and air-dried on stubs with double-sided carbon tape. Shells and radulae for SEM examination were coated with gold–palladium and examined at low accelerating voltage (5–10 kv) in a Hitachi S-570 scanning electron microscope.

The following abbreviations and acronyms are used:

a.s.l. – above sea level;
BMNH – Natural History Museum, London, UK;
L/W – length/width ratio;
NMSA – Natal Museum, Pietermaritzburg, South Africa;
NMW – National Museum of Wales, Cardiff, UK;
RBINS – Royal Belgian Institute of Natural Sciences, Brussels, Belgium;
RMCA – Royal Museum of Central Africa, Tervuren, Belgium;
SAM – South African Museum, Cape Town, South Africa.

TAXONOMY

Family Bulimulidae Tryon, 1867

If the Bulimulinae and Orthalicinae are taken to belong to the same family, then Orthalicidae Albers, 1860 has precedence (Bouchet & Rocroi 2005). However, the Bulimulidae and Orthalicidae are frequently considered to be distinct at family level (Zilch 1959–60; Schileyko 1999), and there is in general considerable uncertainty regarding the relative ranking of supraspecific taxa within the Orthalicoidea—a problem that cannot be resolved until we have a clearer understanding of the phylogenetic relationships of the taxa concerned. Following Herbert and Mitchell (in press), I employ the commonly used name Bulimulidae for a broadly interpreted assemblage of orthalicoid taxa not belonging to the Orthalicidae or Amphibulimidae. At the same time I note that the Odontostominae is also frequently considered a separate family (Zilch 1959–60; Vaught 1989) and, furthermore, that some recent authors have elected also to treat placostyline taxa as a separate family (Neubert & Janssen 2004; Bouchet & Rocroi 2005).

Genus *Prestonella* Connolly, 1929

Prestonella: Connolly 1929: 232. Type species (original designation): '*Buliminus bowkeri*' [*sic*] Sowerby, 1890.

Diagnosis: Shell succineiform to elongate-conical, thin; peristome obliquely tangential, lacking dentition or labral thickening; umbilicus patent but partially concealed by reflected columella; protoconch steep-sided and roundly angular, frequently with more or less straight axial riblets and finer spiral threads; teleoconch sculptured with uneven growth-ridges and sometimes with spiral threads, producing a fine, uneven granulation/reticulation on spire whorls; teeth in central portion of radula monocuspid; jaw stegognathous. Distal reproductive tract relatively simple; penis complex long, including an epiphallus and flagellum; penis retractor muscle short, attached to tip of flagellum; duct of bursa copulatrix long; no other accessory appendages or glands.

Distribution (Fig. 1): Endemic to southern Africa; known only from south-western Lesotho and along the southern edge of the Great Escarpment in South Africa, 1000–1750 m a.s.l.

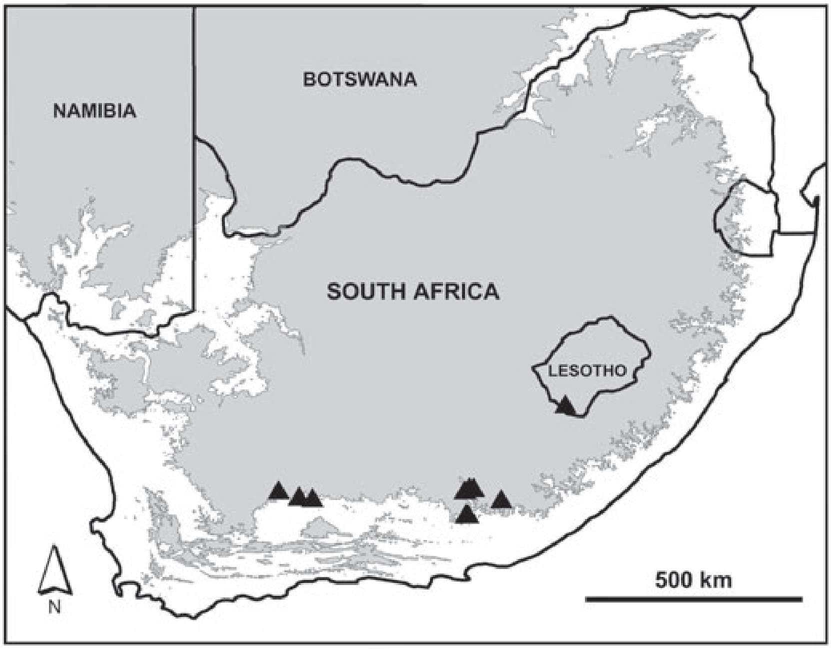


Fig. 1. Distribution of *Prestonella*. The genus is endemic to southern Africa, occurring in south-western Lesotho and along the southern edge of the Great Escarpment in South Africa (1000–1750 m a.s.l.); contour at 1000 m, showing approximate position of Great Escarpment.

Key to species of *Prestonella*

1 Shell buff to pale pinkish-brown (apricot) overlain with white; apex often noticeably darker, orange-brown; length up to 23.25 mm; animal pale buff to yellowish .... **bowkeri**

– Shell yellow-ochre to ochre-brown, apex not or only slightly darker; length up to 15.5 mm 2

2 Shell lacking spiral sculpture; animal dark brown .... **nuptialis**

– Shell with fine spiral threads; animal unknown .... **quadingensis**

Although *Prestonella bowkeri* is generally more elongate than both *P. nuptialis* and *P. quadingensis* (L/W frequently >1.70), there is some overlap in measurements of shell proportions (Table 2). As a result these are not diagnostic and cannot be used in key construction.

TABLE 2

Size and relative proportions of *Prestonella* species.

Species	Max length (mm)	Adult L/W	Body whorl length (% of total length)	Aperture length (% of total length)
bowkeri (N=77)	23.25	1.53–2.0	78.5–87.3	45.3–58.3
nuptialis (N=17)	15.5	1.37–1.69	81.4–90.4	48.2–62.9
quadingensis (N=4)	12.2	1.43–1.55	84.9–87.1	55.8–64.0

Prestonella bowkeri (Sowerby, 1890)

Figs 2–7, 9–11, 19, 25

Bulimus (*Mesembrinus*?) *bowkeri*: Sowerby 1890: 581, pl. 56, fig. 5. Type loc.: ‘Somerset (East), Cape Colony [South Africa]. Forest about 3,000 ft above sea-level (Col. Bowker)’.

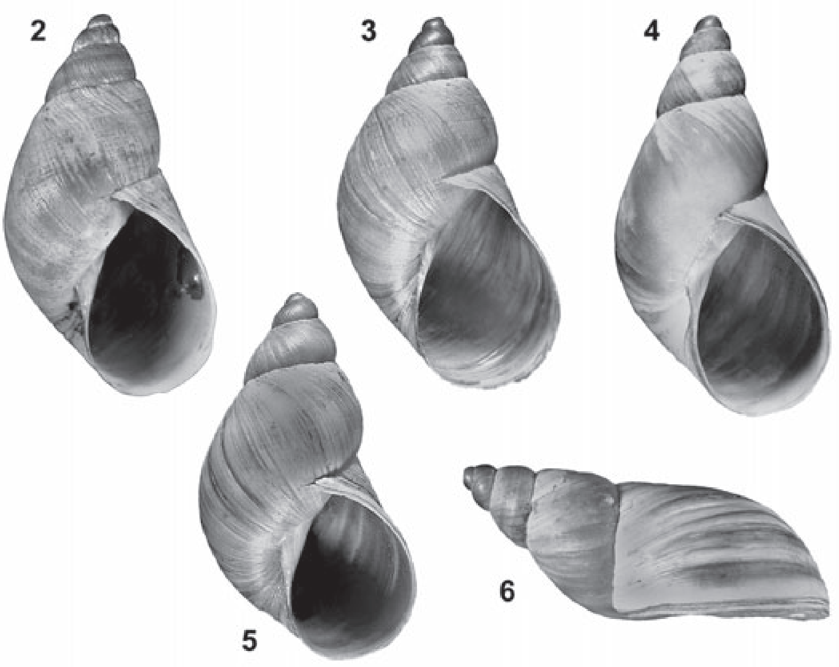
Buliminus (*Pachnodes*) *bowkeri*: Kobelt 1902: 657, pl. 101, fig. 2.

Ena bowkeri: Connolly 1912: 165.

Prestonella bowkeri: Connolly 1929: 232; 1939: 292, pl. 9, figs 25, 29, text-fig. 24 (radula); Barnard 1948: vii.

Description (Figs 2–7): Shell succineiform to elongate-conical, thin; suture weakly to moderately indented. Aperture broadly drop-shaped; upper part of columella lip reflected over and partially covering umbilical region, umbilicus remaining patent but rather narrow; apertural rim strongly oblique, adapical part of outer lip extending almost to mid point of ventral part of body whorl (tangential) and the peristome thus effectively in one plane (Fig. 6); aperture without teeth, denticles or varices.

Sculpture somewhat variable and superficial features frequently badly eroded, such that shells appear more or less smooth and lustreless. In fresh specimens, early part of first teleoconch whorl sculptured for the most part only with irregular, collabral growth-ridges, but these supplemented by uneven, close-set spiral threads soon thereafter; growth-ridges and threads interacting to produce a fine, irregularly granular sculpture over adapical surface of whorls, most noticeable on spire whorls (appearing pitted in worn shells); growth-ridges strongest immediately below suture; occasional intervals between spiral threads stronger than others and appearing as incised spiral lines; some features of spiral sculpture evidently scar-like growth flaws resulting from damage to



Figs 2–6. *Prestonella bowkeri* (Sowerby, 1890): (2) lectotype of *Bulimus* (*Mesembrinus*?) *bowkeri* Sowerby, 1890, length 19.5 mm (BMNH 89.11.4.9); (3) fresh specimen, Glen Avon Falls, length 18.5 mm (NMSA V9816); (4) eroded specimen, Glen Avon Falls, length 20.5 mm (NMSA 2977); (5) Beaufort West specimen, length 17.7 mm (SAM A8171); (6) side view, length 20.5 mm (NMSA 2977).

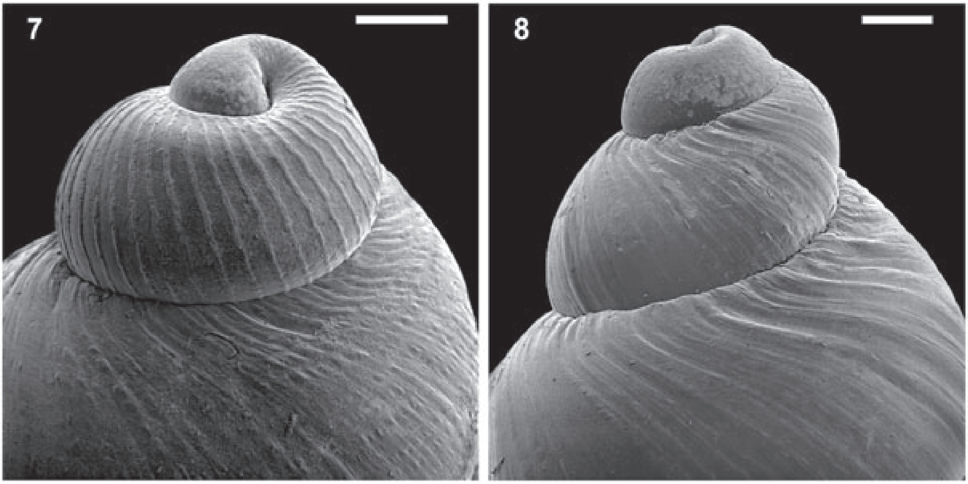
mantle edge; sculpture of later whorls and base weaker, essentially of growth-ridges only.

Colour: Apical whorls corneous orange-brown, becoming paler with growth; surface layer of body whorl whitish, underlying layers apricot-coloured; fresh specimens with a straw-brown periostracum. Periostracum, sculpture and whitish superficial shell layer often completely eroded away (Fig. 4). Head-foot buff to yellow.

Dimensions: Length up to 23.25 mm, width up to 13.5 mm; adult L/W 1.53–2.0; body whorl length = 78.5–87.3% of shell length; aperture length = 45.3–58.3% of shell length (N=77). The material examined comes from two widely separated regions with the following dimensions in the two populations:

- Somerset East: length up to 23.25 mm, width up to 13.5 mm; adult L/W 1.53–1.98; body whorl length = 79.2–87.3% of shell length; aperture length = 46.0–57.7% of shell length (N=50).
- Beaufort West: length up to 19.4 mm, width up to 11.3 mm; adult L/W 1.63–2.0; body whorl length = 78.5–84.5% of shell length; aperture length = 45.3–58.3% of shell length (N=27).

Protoconch (Fig. 7): Diameter approx. 1.6–1.85 mm (Somerset East); 1.85–2.2 mm (Beaufort West), comprising approx. 2.0 whorls; first whorl set at a pronounced angle, rising to start of second whorl which is initially flat-sided with an almost ridge-like



Figs 7, 8. *Prestonella* protoconchs: (7) *P. bowkeri*, Nuweveldberg, Beaufort West (SAM, A8171); (8) *P. nuptialis*, protoconch. Scale bars = 0.5 mm.

apical angle, becoming more evenly convex toward end of whorl; sculptured with widely spaced collabral axial riblets, approx. 0.20 mm apart, riblets about one fifth the width of their intervals; intervals sculptured by numerous close-set spiral striae; riblets usually straight, but somewhat wavy in occasional individuals; specimens from Beaufort West area show strongest protoconch sculpture, in which the change from embryonic to adult sculpture is moderately abrupt and the protoconch–teleoconch junction thus relatively distinct; those from Somerset East (particularly above the Glen Avon falls) with weaker, sometimes almost obsolete protoconch sculpture, but many specimens from this site badly eroded.

Type material: Connolly indicated that the ‘type set’ was in the BMNH, but the type lot contains only one specimen, BMNH 89.11.4.9, ‘Somerset (East), Cape Colony’ [South Africa], length 19.5 mm (Fig. 2). It is here designated lectotype. An additional two paralectotypes are present in RMCA (Glen Avon, Miss Bowker, 97477, 97478).

Type locality: Sowerby stated that the original specimens were collected in ‘forest about 3000 ft [about 900 m] above sea-level’, near Somerset East. Connolly (1912) localised this more precisely as ‘Glen Avon Falls’ and labels associated with additional NMSA material collected in the early 1900s give the locality as ‘The Gorge, Somerset East’—another name for the Glen Avon Falls. It seems likely that Colonel J.H. Bowker and/or his niece Mary Layard Bowker collected the original specimens at this locality. Indeed, descendants of the Bowker family still own ‘Glen Avon’ farm.

Additional material examined: SOUTH AFRICA: *Eastern Cape*: Glen Avon Falls, Somerset East (32°40.887'S: 25°38.13'E), 1000 m a.s.l., on large boulders in forest beside base of falls, D. Herbert, M. Bursey & G. Redman, 19.i.2002 (NMSA V9816, W753); same locality, 1100 m a.s.l., on rock wall above falls, D. Herbert, M. Bursey & G. Redman, 19.i.2002 (NMSA V9818); Somerset East, J. Farquhar and Mrs J.H. Howard (NMSA 2978, B115, W392, W887-8); ‘The Gorge’ Somerset East (NMSA 2977-8, B110-4, B116, W392, W887, mostly collected by Mrs J.H. Howard, 1915). *Northern Cape*: Oukloof, Nuweveldberg, between Fraserburg and Beaufort West [estimated position 32°10'S:21°45'E, approx. 1200–1500 m a.s.l.], Drs Hesse & Boonstra, 1946 (SAM A8171). *Western Cape*: Beaufort West area, Karoo National Park, Rooivalle (32.32553ºS:22.449ºE), 1130 m a.s.l., and Fonteintjieskloof (32.29553ºS:22.17314ºE), 1150 m a.s.l., M. Bursey, i.2004 (NMSA W1479, W1480).

Distribution (Fig. 9): Endemic to South Africa, recorded from Eastern Cape, Northern Cape and Western Cape provinces. Currently known only from three localities, all situated on the southern section of the Great Escarpment, in the vicinity of Somerset East and Beaufort West, at altitudes of 1000–1500 m.

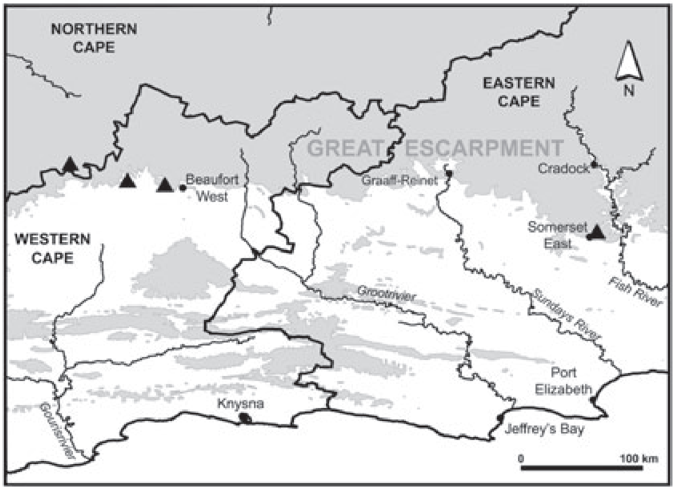
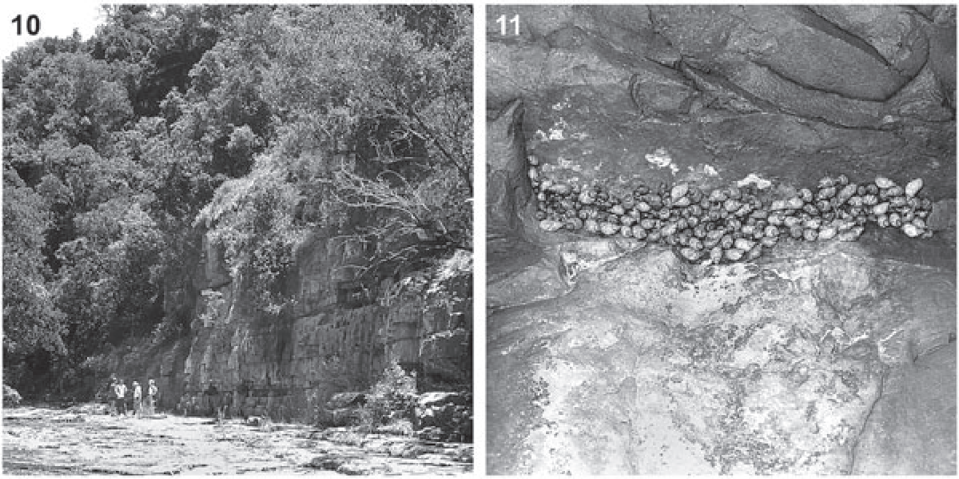

NORTHERN CAPE
EASTERN CAPE
N
GREAT ESCARPMENT
Beaufort West
Graaff-Reinet
Cradock
Somerset East
WESTERN CAPE
Grootrivier
Sundays River
Fish River
Port Elizabeth
Knysna
Jeffrey's Bay
Gouritsrivier
0
100 km

Fig. 9. *Prestonella bowkeri* distribution.

Habitat (Figs 10, 11): Early records provided no habitat information, but recently collected samples suggest very specific habitat requirements. Specimens from both the type locality and the Karoo National Park were found where rivers, in traversing sharp topographical gradients at the edge of escarpments, form waterfalls and have cut steep-sided, wooded/forested gorges or 'kloofs'. The snails are found almost exclusively on near-vertical rock walls above the water course, primarily up-stream of the falls, and on the shaded (south-facing) side. The rock faces are mostly bare of macroscopic vegetation and superficial encrustations, the snails hiding in crevices and under overhangs in the otherwise smooth rock, sometimes in aggregations of more than 100 individuals. The populations seem restricted to the environs of the waterfall, mostly ranging less than

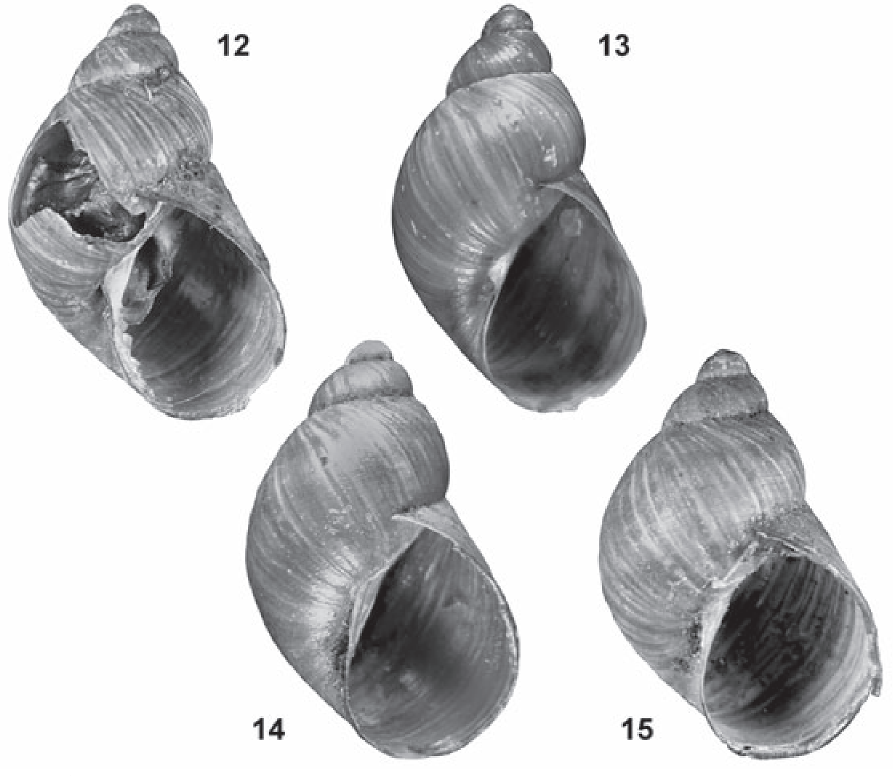


Figs 10, 11. Habitat of *Prestonella bowkeri*, above Glen Avon falls, Somerset East: (10) flat river bed with near vertical rock wall on south-facing bank, (11) cluster of more than 100 individuals under an overhang in the rock wall.

200 m above or below it. The third locality, at Oukloof in the Nuweveldberg, appears also to be a site where a river (Koekemoersrivier) descends an escarpment, but no habitat details were recorded with the specimens.

Although situated in a relatively dry area (rainfall about 300–500 mm per annum, Schulze 1997), orographic phenomena associated with areas of sharp topographical change would be likely to concentrate rainfall and mist at these escarpment-edge localities. The habitats will thus be less xeric than the surrounding eastern mixed Nama Karoo and valley thicket vegetation (Low & Rebelo 1996), and hence the presence of afrotemperate forest and wooded ravines on south-facing slopes. Cooling orographic breezes combined with wind-blown spray from the waterfall and the shaded aspect of the habitat are further likely to ameliorate conditions.

Notes: In the Glen Avon population there appear to be two cohorts of shells, suggesting a biennial lifecycle. In one, the shell is relatively thin, uneroded, and the periostracum is for the most part still present. In the second, the shell is somewhat thicker, and the periostracum and sculpture almost completely eroded. The former probably represent snails hatched during the season of collection and the latter may perhaps be snails that are more than one year old.



Figs 12–15. *Prestonella nuptialis* (Melvill & Ponsonby, 1894) and *P. quadingensis* Connolly, 1932: (12) *P. nuptialis* holotype, length 11.5 mm (BMNH 1905.1.26.29); (13) undamaged specimen, Cradock, length 13.3 mm (NMSA 1592); (14) *P. quadingensis* holotype, length 12.2 mm (NMSA J8135/T2835); (15) paratype, length 11.4 mm (BMNH 1937.12.30.7079-80).

Prestonella nuptialis (Melvill & Ponsonby, 1894)

Figs 8, 12, 13, 16–18, 20–24, 26–28

Buliminus nuptialis: Melvill & Ponsonby 1894: 92, pl. 1, fig. 5. Type loc.: 'Craigie Burn, Somerset East', South Africa, leg. Mrs Mary Layard Barber [née Bowker].
Buliminus nuptialis: Sturany 1898: 602.
Buliminus (*Pachnodes*) *nuptialis*: Kobelt 1902: 762, pl. 111, fig. 22.
Ena nuptialis: Connolly 1912: 172.
Prestonella nuptialis: Connolly 1939: 293.

Etymology: The origin of this somewhat unusual species name is explained by a note with the paratype at the RMCA, which states 'found by goddaughter and sent to me on the eve of her wedding day'; the initials are unclear, but could well be E.L.L. of Edgar L. Layard, who was indeed Mary Bowker's godfather.

Description (Figs 8, 12, 13): Shell succineiform to bulimiform, thin; suture weakly to moderately indented. Aperture ovate to roundly D-shaped; upper part of columella lip reflected over umbilical region, but umbilicus remaining relatively widely patent; apertural rim obliquely tangential, and peristome thus in one plane; aperture without teeth, denticles or varices. Sculpture almost devoid of spiral elements (except on protoconch, see below), comprising only relatively strong, somewhat irregular rounded growth-ridges, strongest below suture and somewhat sinuous in this region.

Colour: Shell translucent when fresh, overlain by yellow-ochre to ochre-brown periostracum with irregular darker and lighter bands corresponding with growth-ridges; apex usually only slightly darker; periostracum and underlying shell often heavily eroded, particularly near apex; frequently with adherent particles of debris. Head-foot dark brown.

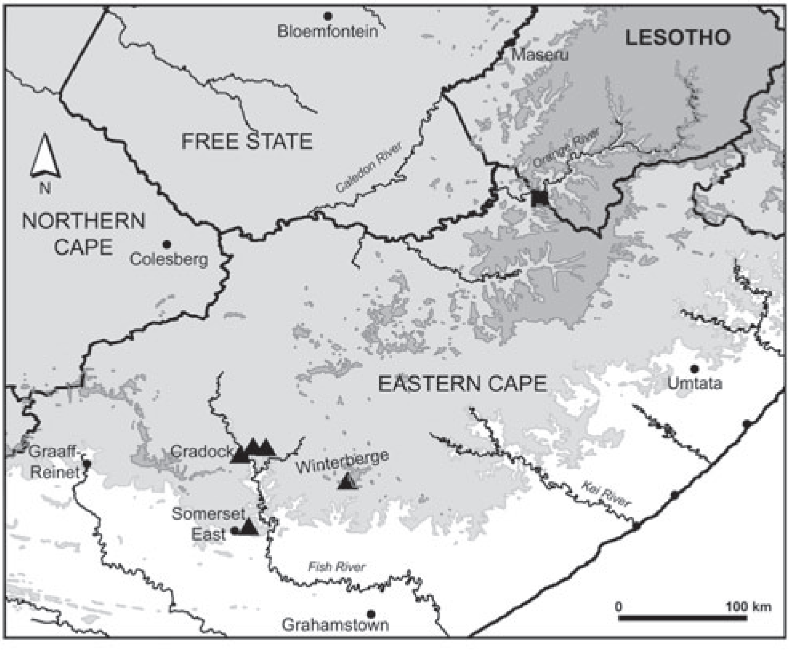

Bloemfontein
LESOTHO
Maseru
FREE STATE
Caledon River
Orange River
N
NORTHERN CAPE
Colesberg
EASTERN CAPE
Umtata
Graaff-Reinet
Cradock
Winterberge
Somerset East
Kei River
Fish River
0
100 km
Grahamstown

Fig. 16. Distribution of *Prestonella nuptialis* (▲) and *P. quadingensis* (■).

Dimensions: Length up to 15.5 mm, width up to 10.0 mm; adult L/W 1.37–1.69; body whorl length = 81.4–90.4% of shell length; aperture length = 48.2–62.9% of shell length (N=17).

Protoconch (Fig. 8): Diameter 1.5–1.75 mm, comprising 1.75–2.0 whorls; basic shape similar to that of *P. bowkeri*, but lacking axial riblets; fine surface detail eroded in most specimens, but traces of microscopic spiral striae present in some; junction between protoconch and teleoconch usually not well defined.

Holotype: SOUTH AFRICA: *Eastern Cape*: BMNH 1905.1.26.29, 'Craigie Burn', Somerset East, J.H. Ponsonby Esq. [originally collected by Mrs Mary Layard Barber (née Bowker), and sent by E.L. Layard]; length 11.5 mm (Fig. 12).

Paratype: 'Craigie Burn', Somerset East (RMCA 26584).

Type locality: The locality cited in the original description, 'Craigie Burn', is a farm on the eastern slopes of the Bosberg, south-east of the hill 'Graskop' and immediately north of 'Avon Heights' farm, co-ordinates 32°41.1'S: 25°40.7'E, altitude approx. 1000 m a.s.l.

Additional material examined: SOUTH AFRICA: *Eastern Cape*: Cradock area, Elandsberg Mountain (32°07.488'S:25°42.348'E), approx. 1450 m a.s.l., just below summit, on southern slope, D. Herbert, M. Bursey & G. Redman, 23.i.2002 (NMSA V9781); Cradock area, inselberg south of Tarkastad road, near 'Plankfontein' farm (32°07.822'S:25°47.795'E), 1530 m a.s.l., just below summit on south-facing slope, D. Herbert, M. Bursey & G. Redman, 24.i.2002 (NMSA V9778); Cradock area, 'found in narrow fissures in the rocks on the mountain tops' (NMSA 1592); Cradock area, Elandsberg Mountain (W901and NMW); Cradock (NMSA B117, V5275); Cradock, J. Farquhar (NMSA W437); Cradock, (RMCA 26585 and RBINS); Adelaide area, Fenella Falls (32.367°S:26.367°E), in crevices in rocks behind high waterfall, M. Bursey, v.2007 (NMSA W5507).

Distribution (Fig. 16): Endemic to South Africa, and recorded only from Eastern Cape province, in the environs of Somerset East and Cradock, and the Winterberge mountain range, at altitudes of 1000–1600 m a.s.l. In the Somerset East area it is only known from the type locality and has not been collected in this area since its description.

Habitat (Figs 17, 18): Living specimens have recently been collected at two localities. Firstly near the summit of two 'inselbergs' in the Cradock area, and secondly at the Fenella Falls in the Winterberge. At the Cradock site, the specimens were found wedged in crevices and under overhangs in the near vertical face of a narrow band of reddish mudstone just below the summit of the mountains. The aspect was largely south-facing and thus for the most part shaded. The rock was mostly bare of superficial encrustations. A note stating 'found in narrow fissures in the rocks on the mountain tops around

17

18

Figs 17, 18. Habitat of *Prestonella nuptialis*, Elandsberg, Cradock: (17) Elandsberg with its summit in cloud, on a day when no rainfall was recorded in the surrounding landscape; (18) vertical rock faces near summit, with crevices and overhangs in which the species lives.

Cradock' associated with specimen lot NMSA 1592 indicates that W. Farquhar's material cited by Connolly (1939) was collected in a similar habitat. In contrast, the Fenella Falls site closely resembled sites at which *P. bowkeri* has been found—a shaded, gorge-like habitat with a high waterfall, the snails being found in crevices in bare rock walls in the immediate environs of the waterfall. Nothing is known of the precise habitat in which the type specimens were collected at 'Craigie Burn'.

As with the habitat of *P. bowkeri*, orographic phenomena associated with these sites will mean that they provide moister habitats than those of the surrounding landscape matrix. In overcast weather, the tops of Karoo inselberg mountains frequently project into the cloud layer (as they did when the Cradock material was collected, Fig. 17) and thus will be subject to moist conditions, while the intervening, lower-lying land remains dry and typical of the Nama Karoo biome (Low & Rebelo 1996). Although not measured, the temperature near the Elandsberg summit was significantly cooler, and made more so by wind. At Fenella Falls, mist associated with the Winterberge mountains combined with wind-blown spray from the waterfall and the shaded aspect of the habitat are likely result in relatively mesic conditions.

Notes: Differs from *P. bowkeri* in being smaller and generally broader with more convex whorls (but adult L/W ratios overlap, Table 2), and in lacking both fine granular sculpture on the adapical surface of the spire whorls and axial riblets on the protoconch. The living animal is of a much darker colour than that of *P. bowkeri*. *P. quadingensis* (below) is identical, except that it possesses fine spiral sculpture on later whorls, has axial riblets on the protoconch and is perhaps slightly more obese.

Prestonella quadingensis Connolly, 1929

Figs 14–16

Prestonella quadingensis: Connolly 1929: 233, pl. 14, fig. 25; 1939: 293; Bruggen 1985: 292. Type loc.: 'Basutoland, Quading' [= Lesotho, Quthing (Moyeni)], leg. E. Ford.

Description (Figs 14, 15): Extremely similar to *P. nuptialis*, from which it differs chiefly in the presence of fine, spiral threads on the teleoconch whorls, and axial riblets on the protoconch. The whorls are also perhaps slightly more obese, but ratios of shell proportions overlap extensively with those of *P. nuptialis* (Table 2). Colour of living animal unknown.

Dimensions: Length up to 12.2 mm, width up to 8.0 mm; adult L/W = 1.43–1.55; body whorl length = 84.9–87.1% of shell length; aperture length = 55.8–64% of shell length (N=4).

Protoconch: Diameter approx. 1.6 mm, comprising approx. 2.0 whorls; basic shape and sculpture similar to that of *P. bowkeri*; badly eroded, but retaining traces of strong, widely spaced axial riblets and close-set microscopic spiral striae.

Holotype: LESOTHO: Quthing [Moyeni], leg. E. Ford, *ex* Farquhar collection, *ex* Albany Museum (NMSA J8135/T2835), length 12.2 mm (Fig. 14).

Paratypes: LESOTHO: 'Quading' leg. E. Ford (BMNH 1937.12.30.7079-80), two specimens (Fig. 15).

Additional material examined: LESOTHO: Quthing [Moyeni], leg. E. Ford, *ex* Albany Museum (NMSA J8086).

Distribution (Fig. 16): Known only from the type locality in south-western Lesotho, at approx. 1750 m a.s.l.

Habitat: Apart from the fact that the type locality lies at about 1750 m a.s.l., within the grassland biome, nothing is known of the habitat of this species.

Notes: It seems doubtful that this taxon is genuinely distinct from *P. nuptialis*. In view of the distance between the populations and their probable genetic isolation, some geographical variation in shell form is perhaps to be expected. The axial ribbing on the protoconch of *P. quadingensis* and its absence in *P. nuptialis* may not be significant since this character varies considerably between and within *P. bowkeri* populations. A definitive statement on the validity of this species must await the discovery of additional material for more in-depth study.

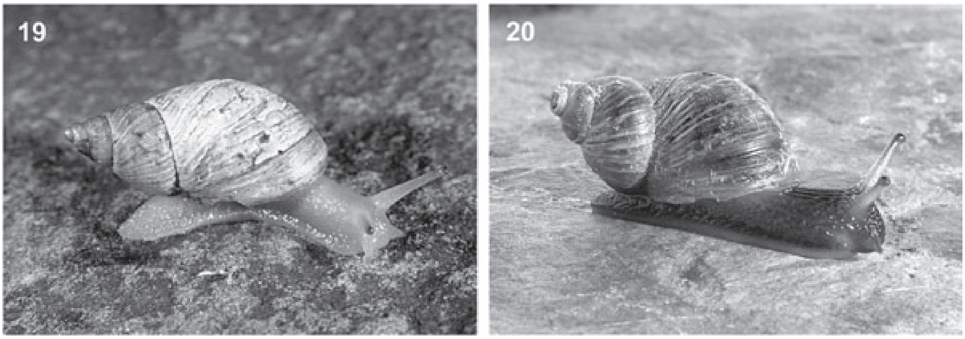
DISCUSSION

Morphology of soft parts

Anatomical observations on the jaw, radula, pulmonary cavity, and reproductive tract of *P. bowkeri* are provided by Herbert and Mitchell (in press), and their significance with regard to the phylogenetic relationships of the genus discussed in detail. A summary of these morphological features is provided below, together with comparative remarks on the anatomy of *P. nuptialis*. No preserved material of *P. quadingensis* is available.

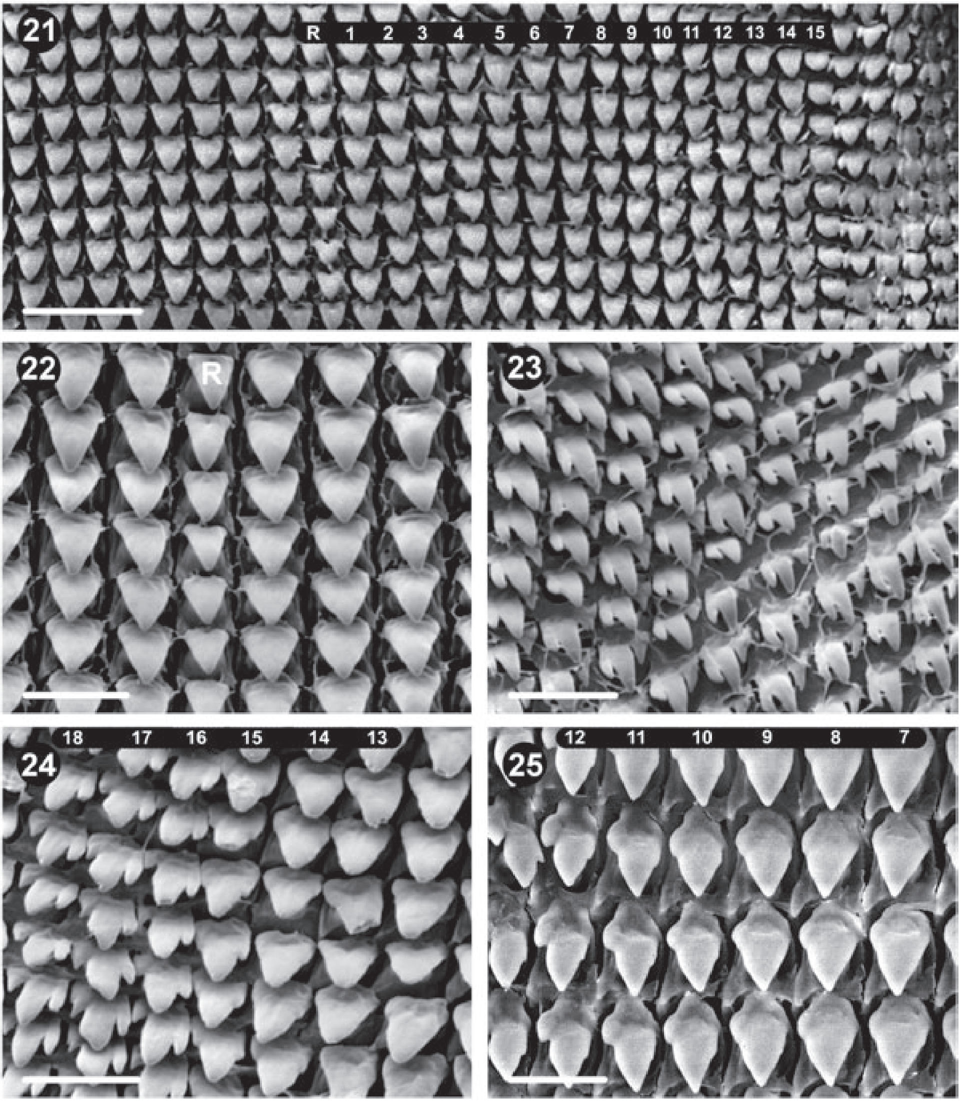
External features (Figs 19, 20): Head-foot more or less uniformly pale apricot-buff to yellow in *P. bowkeri*, dark brown in *P. nuptialis*; upper and lower tentacles well-developed, but not particularly long; genital aperture ventral and slightly posterior to right ommatophore; peripodial groove not evident; hind end of foot blunt ending; sole not obviously subdivided longitudinally, but its lateral margins may be more deeply pigmented.

Radula (Figs 21–25): Dentition extremely fine; radula up to 3.4 mm long and 1.1 mm wide, with up to 230 transverse rows of teeth, each with up to 100 teeth, depending on size of animal. Rows more or less perpendicular to mid-line in central region, curving slightly backwards or forwards laterally (probably related to specimen mounting), but not V-shaped. In *P. bowkeri* tooth form smoothly intergrades across width of radula and there is thus no clear distinction between lateral and marginal teeth (Fig. 25), approximate formula R+L(10–11)+M±30. In *P. nuptialis* the boundary between the laterals and marginals is somewhat clearer (at least under SEM) (Fig. 24) and the formula is approxi-



Figs 19, 20. *Prestonella bowkeri* and *Prestonella nuptialis*, living specimens: (19) *P. bowkeri*, shell length 18.0 mm, Glen Avon Falls (NMSA V9816); (20) *P. nuptialis*, shell length 13.0 mm, Fenella Falls (NMSA W5507).

mately R+L15+M(20–30). Details of tooth morphology are provided by Herbert and Mitchell (in press). The most significant feature is the monocuspid form of the rachidian and lateral teeth. Although in other respects the *Prestonella* radula is typical of phytophagous species, the lack of secondary cusps on the teeth in the central field is a somewhat unusual feature. Breure and Gittenberger (1982) identified such monocuspid teeth as a structural, diet-related modification associated with a rock-scraping mode of feeding, and showed it to be an adaptive character occurring in a number of unrelated families,



Figs 21–25. *Prestonella* radulae: (21–24) *P. nuptialis* (NMSA V9778): (21) central field and inner marginals (rachidian and laterals numbered), scale bar = 50 µm; (22) rachidian (R) and inner laterals, scale bar = 25 µm; (23) outer marginals, scale bar = 25 µm; (24) latero-marginal transition, scale bar = 25 µm; (25) *P. bowkeri* (NMSA V9816) latero-marginal transition, scale bar = 25 µm.

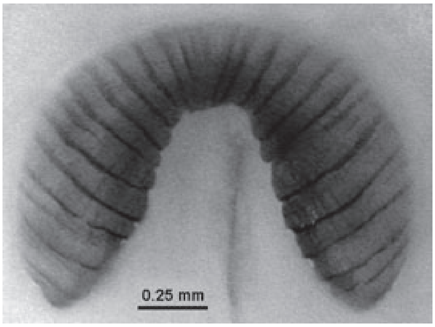


Fig. 26. *Prestonella nuptialis* jaw, extended through mouth after drowning (NMSA W5507).

including other Bulimulidae. Although the feeding behaviour of *Prestonella* has not been observed, this is entirely consistent with the microhabitat in which all species occur, namely bare rock surfaces, and the heavy wear evident on the anterior radula teeth.

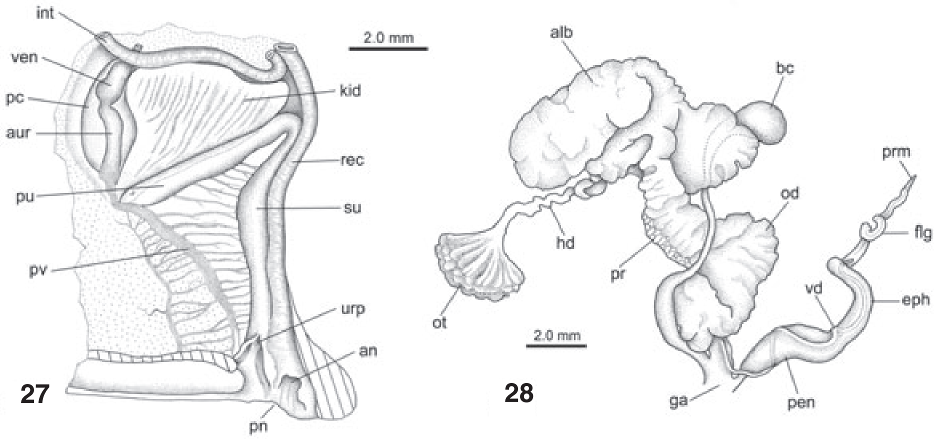
Jaw (Fig. 26): Crescentic to almost U-shaped, composed of fused, imbricating chitinous plates (stegognathous), translucent corneous yellow to brown; central plate broadly triangular; lateral plates elongate and with more or less parallel sides, 7–12 on each side, the inner of two plates overlapping its outer neighbour.

Pulmonary anatomy (Fig. 27): Typically sigmurethrous. Essentially the same in both *P. bowkeri* and *P. nuptialis*, except that in the latter the kidney is somewhat broader and the main pulmonary vein more oblique on account of the less elongate shell. Kidney short and trigonal, bright orange in living specimens; secondary ureter closed for most of its length except in distal region, just inside pneumostome, where it opens to form a V-shaped notch.

Genital system: The distal reproductive tract is relatively simple, lacking auxiliary structures (e.g., dart sac, accessory glands, appendages, and stimulatory organs), but including an epiphallus and flagellum in the penis complex. A detailed description of the reproductive tract of *P. bowkeri* is provided by Herbert and Mitchell (in press). That of *P. nuptialis* is essentially the same (Fig. 28), although its penis complex and sperm-oviduct are somewhat less elongate and the vas deferens follows a more twisted course along the penis.

Conservation

The genus *Prestonella* appears to exhibit a relictual distribution associated with the southern edge of the Great Escarpment in South Africa and Lesotho. The species are evidently habitat specialists, a fact no doubt contributing to the very few distribution records available. The habitats favoured represent isolated mesic micro-environments in an otherwise more xeric matrix. Such habitats are created by a combination of aspect, topography and orographic climatic phenomena that result in a localised increase in humidity levels, either where water courses descend steep escarpments, or near the summits of Karoo inselbergs. Evidently bulimulid species in the Galapagos Islands are also frequently habitat specialists, with limited distributions restricted to specific micro-climates or vegetation types (Coppois & Wells 1987; Coppois 2003).



Figs 27, 28. *Prestonella nuptialis* (NMSA V9778): (27) pulmonary anatomy (abbreviations: an – anus, aur – auricle, int – intestine, kid – kidney, pc – pericardium, pn – pneumostome, pu – primary ureter, pv – pulmonary vein, rec – rectum, su – secondary ureter, urp – ureteric pore, ven – ventricle); (28) genital anatomy (abbreviations: alb – albumen gland, bc – bursa copulatrix, eph – epiphallus, flg – flagellum, ga – genital atrium, hd – hermaphrodite duct, od – oviduct, ot – ovotestis, pen – penis, pr – prostate gland, prm – penis retractor muscle, vd – vas deferens).

The very nature of their specialist habitats suggests that the distributions of the species must be highly fragmented. Nonetheless, the known extent of occurrence of *P. bowkeri* is relatively broad, extending from west of Beaufort West to the Somerset East area (about 350 km), even though its area of occupancy within this region is likely to be far more limited. In the case of *P. nuptialis*, only three localities in a relatively small extent of occurrence are currently recorded, but inselberg habitats in the Karoo are common and the paucity of distribution data available results almost certainly from the inaccessibility of these habitats and lack of collecting, rather than genuine rarity. Its extent of occurrence may be substantially greater than the available data suggests. Our knowledge of the distribution of *P. quadingensis* is even more limited (known only from the type locality in south-western Lesotho and without habitat data), but the uncertainty regarding its validity as a taxon distinct from *P. nuptialis* must be borne in mind. In terms of the current IUCN criteria, all three species are probably best considered *Data Deficient*. Information permitting an informed categorisation at a more specific threat level is not at present available.

The above notwithstanding, it is clear that, with specialised habitats and fragmented distributions, all *Prestonella* species are likely to be adversely affected by anthropogenic environmental change. Not the least of such threats is likely to be climate change. Modelling the impact of a doubling of global CO_2 concentrations (predicted to cause a 2ºC temperature increase) on a sample of South African animal taxa, Erasmus *et al.* (2002) have shown that climate change is likely to result in both range contraction and an eastward range shift for many species in the drier western and central parts of South Africa, with the possibility of extinction for habitat specialists. For taxa such as *Prestonella* species with highly fragmented, insular distributions, such impacts may have serious consequences. Their ability to track favourable environmental conditions, as these move eastwards, will be constrained by their specialised habitat requirements and very limited capacity for dispersal. Furthermore, if climate change is accompanied by increased aridity—a possibility in the southern African interior (Hulme *et al*. 2001; New 2002)—there are likely to be additional consequences for taxa already restricted to isolated mesic refugia in a low-rainfall biome. Any increase in the duration of flow interruptions in the water courses that sustain populations in peri-riverine habitats is likely to have a negative impact. Similarly, inselberg populations of *P. nuptialis* are evidently already confined to the summits and cannot migrate to higher altitudes to escape the impact of increasing temperature or aridity. Thus, human impact may have serious indirect implications for the survival of both species. Since *Prestonella* represents the sole surviving African element of a Gondwanan lineage that has persisted in isolation in post-Gondwanan Africa for more than 95 million years (Herbert & Mitchell in press), these threats to its continued existence resulting from human-induced change are not without consequence. *Prestonella* is a significant component in the phylogenetic diversity of the African fauna.

ACKNOWLEDGEMENTS

For assistance in the field I thank the Brown family at 'Glen Avon' farm (Somerset East), the Michaud family at 'Plankfontein' farm (Cradock), Guy Redman (now at Durban Natural Science Museum) and particularly Mary Bursey (East London Museum), who planned our field work in the Eastern Cape and collected additional material at Fenella Falls and in the Beaufort West area. Linda Davis skilfully prepared the anatomical illustrations from my *camera lucida* drawings. I also thank Jon Ablett and Kathie Way for providing access to BMNH type material, Liz Hoensen for facilitating the loan of SAM specimens, and the University of KwaZulu-Natal for use of the facilities at its Centre for Electron Microscopy. This research was funded largely through a grant from the National Research Foundation, South Africa.

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